Climate and land use changes will degrade the distribution of Rhododendrons in China

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HIGHLIGHTS

- The combined impacts of climate and land use change on Rhododendrons in China
- Rhododendrons will be generally negatively affected by climate and land use change.
- Narrow-ranging Rhododendrons are facing high risk of extinction.
- Climate change is expected to override the effects of human uses of the land.

GRAPHICAL ABSTRACT

Potential impacts of climate and land use changes on species

ABSTRACT

Biodiversity loss and variation in species responses to climate and land use change have been found across broad taxonomic groups. However, whether species from the same taxonomic group with distinct geographical ranges will respond differently is poorly understood. The aim of this study is to predict the potential impacts of future climate and land use change on the distribution of narrow- and wide-ranging Rhododendron species, and estimate their relative contribution in China. We applied the presence-only ecological niche model MaxEnt to predict the distribution of 10 narrow-ranging and 10 wide-ranging Rhododendron species for the year 2070, using three general circulation models and three scenarios of climate and land use change. We measured the predicted distribution change of each species using change ratio, distance and direction of core range shifts, and niche overlap using Schoener's D. We found that the distribution areas of six narrow-ranging species would decrease, of which one species would go extinct. The remaining four narrow-ranging species would experience range expansion. Distribution of all the wide-ranging Rhododendron species would decrease. All Rhododendrons will shift to the northwest. We conclude that Rhododendron species generally will be negatively affected by the climatic and land use change expected in 2070 from the three scenarios evaluated in this study, but some narrow-ranging species may be positively influenced. Narrow-ranging Rhododendron species are more vulnerable

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compared to wide-ranging Rhododendron species. This study demonstrated that the effects of climate and land use change on alpine and subalpine plant species is species-specific, thereby strengthening our understanding of the impacts of climate and land use change on plant distribution.

1. Introduction

Rapid climate change has resulted in distributional changes for a wide range of taxa (Parmesan, 2006; Chen et al., 2011). In general, species are predicted to shift poleward in latitude and upward in elevation as global temperatures increase (Parmesan and Yohe, 2003; Lenoir et al., 2008). If current greenhouse emission trajectories continue, many species, especially narrowly distributed species with small populations, may go extinct over the next century (Pearson et al., 2014), although extinction estimates differ widely depending on the taxa, spatial scale, and methods used (Frishkoff et al., 2016).

Apart from climate change impacts, human-caused habitat loss and fragmentation (mainly through land use change) has long been considered a primary cause for biodiversity loss and ecosystem degradation worldwide (Foley et al., 2005; Oliver and Morecroft, 2014). The land use change includes deforestation, road construction, agricultural encroachment, dam building, irrigation, mining, expansion of urban environments, and other activities. The cumulative or synergistic interactions between climate change and human land use are believed to have an even greater impact on biodiversity over the coming century (Sala et al., 2000; Brook et al., 2008). Therefore, predicting species' responses to climate and land use change is becoming increasingly important for biodiversity conservation. Key questions for the management of sustainable landscapes are whether a species is likely to be able to persist in a landscape that is undergoing a certain degree of habitat loss in combination with changing climatic conditions, or whether this species will be able to migrate to new regions as they become climatically suitable (Travis, 2003). A number of studies have emphasized the importance of integrating climate and land use change when studying change in species distributions into the future (Sala et al., 2000; Sirami et al., 2017). Nevertheless, the effect of climate and land use change is frequently studied in isolation, with the combined effects of climate and land use change on

biodiversity and the distribution of particular species remain poorly understood (Sirami et al., 2017; Titeux et al., 2016).

In recent years, geographical range size has been used as a proxy measure for predicting extinction risk, as well as to prioritize species for conservation actions in the face of rapid global environmental change (Thuiller et al., 2005; Pompe et al., 2008; Gallagher, 2016). The range of resources that a species use (i.e. niche breadth) determines its geographical range (Slatyer et al., 2013). There is substantial recent evidence, from a variety of taxa, supporting the theory that narrow-ranging species are declining more quickly, or are more vulnerable to climate change and habitat loss than their broader niche relatives (Purvis et al., 2000; Walker and Preston, 2006; Yu et al., 2017a). Species with a small geographical range size, as is the case with many endemic species, could be more sensitive or vulnerable to climate change due to lack of plasticity and insufficient genetic variation to respond to novel selection pressure (Sheth and Angert, 2014). While broadly distributed species with large population sizes, which usually have wide climatological niches, may be buffered against extinction due to their evolved tolerance to a broad range of climatic conditions (Pearson et al., 2014; Yu et al., 2017a). Meanwhile, narrowly distributed species are more likely to be threatened by land use change if they are restricted to a single habitat type, and thus at higher risk of experiencing habitat loss (Köster et al., 2013). The relatively low effect of land use change on widely spread species may also be due to their ability to exploit a wide range of ecological niches (Harcourt et al., 2002; Cleary and Mooers, 2006). Biodiversity loss and variation in species response to environmental change is seen in many different taxonomic groups (Hickling et al., 2006; Pompe et al., 2008), but what is known about the response within taxonomic groups? Is there any interspecific variation in response to environmental change? Will narrow-ranging and wide-ranging species of the same taxonomic group will respond differently to change in climate and land use? And if they do respond differently, what is the difference?

The genus Rhododendron, comprising about 1025 species, forms a major component of alpine and subalpine ecosystems in the Himalayas. The Himalayan region has been recognized as one of the most fragile zones in the world, and is experiencing large change due to climate and land use change (Xu et al., 2009; Kumar, 2012). The Rhododend*n* genus is the only group of plants that covers a continuum from the subalpine up to the alpine zones, maintaining biological sustenance in the Himalayas. Rhododendrons play a vital role in slope stabilization and watershed protection in the Himalayas, where many of Asia's major rivers originate (Gibbs et al., 2011). However, Rhododendrons are among the most neglected groups of plants in terms of scientific inquiry (Kumar, 2012). It is worth to note that Rhododendron species have quite distinct distribution ranges, some species occurring throughout the entire Himalayas, whilst others are highly restricted to small region, such as rocks and boulders of the mountain top (Gibbs et al., 2011). In view of the status as a 'big genus' and it's various distributional ranges, Rhododendron species are considered to be excellent candidates for exploring the difference of narrow- and wide-ranging species in response to climate and land use change. Predicting the distribution of narrow- and wide-ranging Rhododendron species under climate and land use change would, therefore, help us understand the evolution and diversification of flora in the light of global change, as well as provide insights for

Table 1
List of Rhododendron species considered in this study.

Code	Species name	Geographic range (km^2)	Elevation range (m)
N1	*R. changii*	11	2000–3000
N2	*R. praevernum*	15	1350–2350
N3	*R. rufescens*	17	3800–4500
N4	*R. clementinae*	18	3200–4100
N5	*R. coeloneurum*	18	1200–2300
N6	*R. kwangtungense*	18	800–1600
N7	*R. viridescens*	18	3000–3400
N8	*R. impeditum*	21	2500–4600
N9	*R. tutcherae*	22	1200–2000
N10	*R. adenopodum*	36	1100–2200
W1	*R. simsii*	526	500–2700
W2	*R. decorum*	328	1000–4200
W3	*R. racemosum*	263	1500–3500
W4	*R. mariesii*	248	600–1500
W5	*R. ovatum*	242	<1000
W6	*R. delavayi*	180	1400–1800
W7	*R. stamineum*	179	500–1600
W8	*R. rubiginosum*	171	2800–4200
W9	*R. augustinii*	151	1300–3000
W10	*R. aganniphum*	146	2700–4700

N: narrow-ranging species, W: wide-ranging species.

Species names

Narrow-ranging species

- *R. changii*
- *R. praevernum*
- *R. rufescens*
- *R. clementinae*
- *R. coeloneurum*
- *R. kwangtungense*
- *R. viridescens*
- *R. impeditum*
- *R. tutcherae*
- *R. adenopodum*

Wide-ranging species

- *R. simsii*
- *R. decorum*
- *R. racemosum*
- *R. mariesii*
- *R. ovatum*
- *R. delavayi*
- *R. stamineum*
- *R. rubiginosum*
- *R. augustinii*
- *R. aganniphum*

Fig. 1. Locations of 20 narrow- and wide-ranging Rhododendron species used in this study.

conservation planning in the strategies required to maintain the sustainable alpine and subalpine ecosystem in the future. In this study, we aim to (1) predict distribution of narrow- and wide-ranging Rhododendron species under climate and land use change, and (2) estimate the relative contributions of climate and land use on the spatial distribution of narrow-ranging and wide-ranging Rhododendron species.

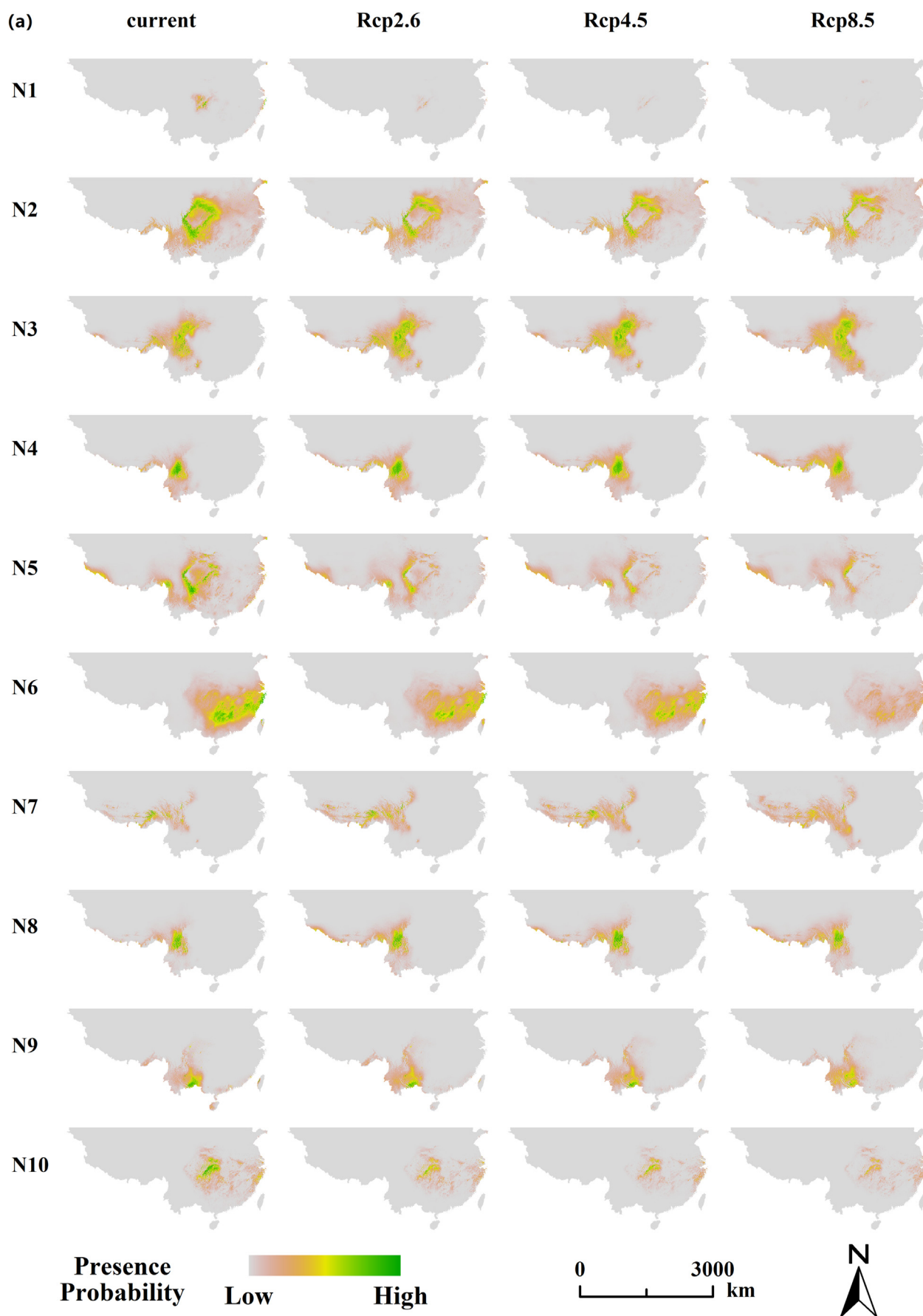## 2. Materials and methods

2.1. Study area and species data

China harbors 571 Rhododendron species, which are widely distributed across most regions (except Xinjiang and Ningxia provinces) (Ma et al., 2014). We collected Rhododendron presence records from seven Chinese herbaria and botanical museums (for more details, see Yu et al., 2015). Since high locational accuracy is required for studying plant species distribution, we excluded all records presenting only a general description of the location (e.g. mentioning only a county or a mountain). Our resulting dataset, covering 406 species, comprises 13,126 geo-referenced records, with each record having a spatial uncertainty of <1 km. In this study, we selected a total of 2628 location records from 20 species (see selection criteria below), which were pooled into narrow- and wide- ranging groups (Table 1), locations of the 20 species see

Fig. 1. The selection was based on the combination of the following criteria: (1) endemism: species are endemic to China, (2) sampling design: samples for included species should be taken from >10 localities with each sample at least 2 km apart in order to lessen the spatial autocorrelation effect, and (3) range size: we projected all species records using a Asia North Albers Equal-Area Conic projection, and calculated the geographical range size of each species as frequency of occurrences of each species in a 1×1 km grid over the whole of China. We then ranked the species based on their geographical range sizes, and selected the 10 most narrow ranging and 10 most wide-ranging species.

2.2. Climate data and climate change scenarios

We initially downloaded 19 bioclimatic variables for current climatic conditions (average for 1950–2000) from the WorldClim 1.4 database (Hijmans et al., 2005), with a 30 arc-seconds (~1 km) resolution. Based on the physiology and life history requirements of Rhododendrons, we selected a set of climatic variables useful for predicting Rhododendrons distribution (Yu et al., 2017a). To deal with collinearity, we performed a Pearson correlation analysis, and obtained six climatic variables ($r < 0.7$) to model the current distribution of each species. These variables included: isothermality (Bio3), temperature seasonality (Bio4), minimum temperature of coldest month (Bio6), annual precipitation

(a)

| | current | Rcp2.6 | Rcp4.5 | Rcp8.5 |

Fig. 2. Distribution maps (presence probability) of the narrow-ranging (a) and wide-ranging (b) groups under current and future (RCP 2.6, RCP 4.5, and RCP 8.5 in 2070) climate and land use conditions. Species codes N1 to N10, and W1 to W10 are explained in Table 1.
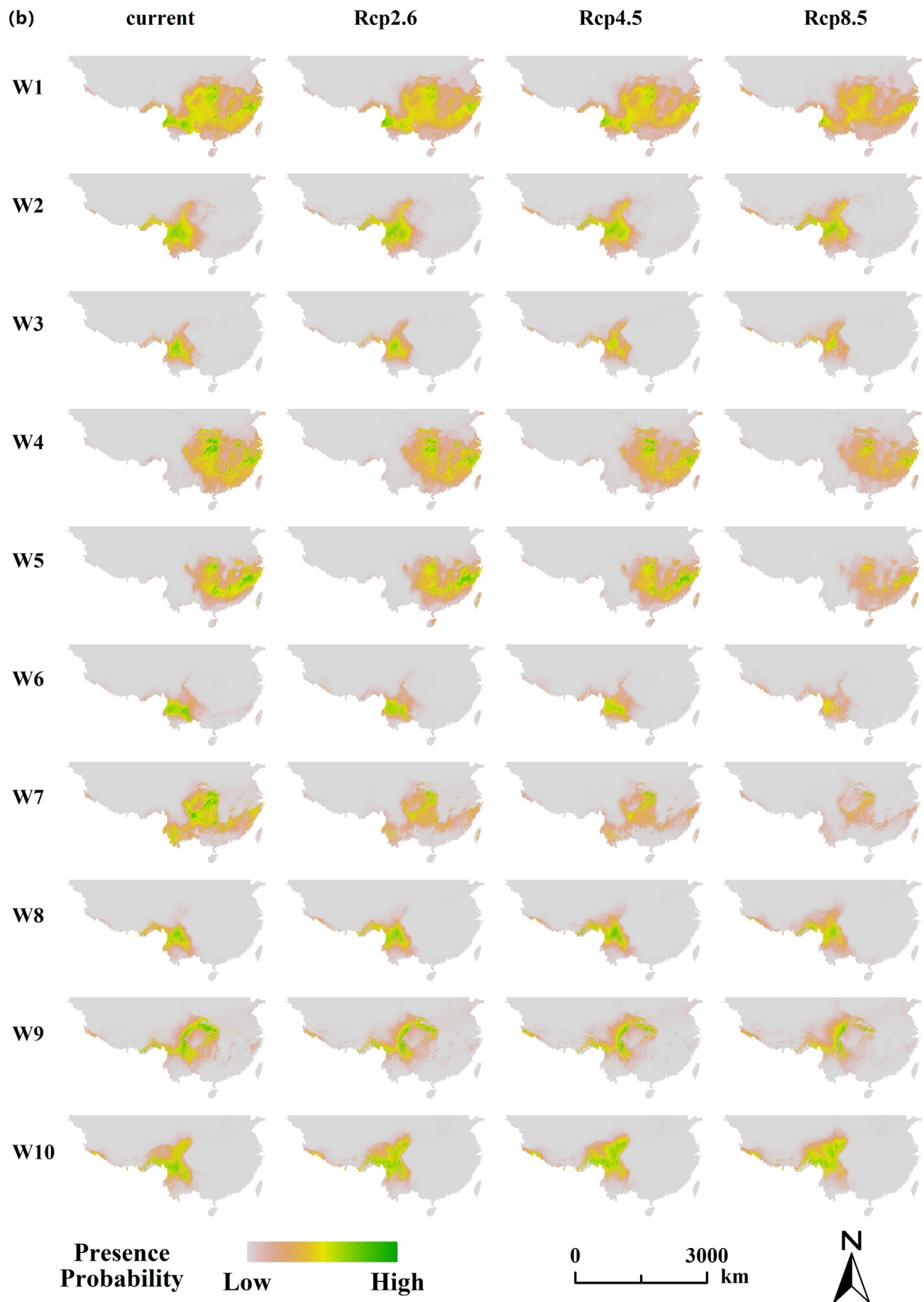
Fig. 2 (*continued*).

(Bio12), precipitation of wettest month (Bio13), and precipitation of driest month (Bio14).

With an aim of capturing plausible variations in future climate (Taylor et al., 2012), we used the same bioclimatic variables from three widely used general circulation models (GCMs) in China (Ye et al., 2018), comprising the Beijing Climate Center Climate System Model (BCC-CSM1-1), Community Climate System Model (CCSM4), and Hadley Global Environment Model 2 - Earth System (HadGEM2-ES), to project future species distributions (average for 2061–2080, hereafter referred to as 2070). The GCMs output was downscaled and calibrated (bias corrected) using WorldClim 1.4 as baseline 'current' climate (http://www.worldclim.org/cmip5_30s).

For each GCM, we used three emission scenarios (representative concentration pathways: RCP 2.6, RCP 4.5, and RCP 8.5) to represent the most optimistic and most pessimistic concentrations of glasshouse gases (GHG) over the next few decades (Weyant et al., 2009). RCP 2.6 is the lowest GHG concentration pathway in which radioactive forcing (global energy imbalances) levels reach 3.1 W/m^2 by mid-century and drops 2.6 W/m^2 by 2100. RCP 4.5 is a stabilization scenario in which the total radiative forcing reaches to 4.5 W/m^2 by 2100 and stabilizes due to the employment of a range of technologies and strategies for reducing GHG emissions. Likewise, RCP 8.5 also represents stabilization by 2100, this time at 8.5 W/m^2 by 2100 (van Vuuren et al., 2011).

2.3. Land use data and land use change scenarios

We obtained current and future land use data with 30 m resolution from the Finer Resolution Observation and Monitoring-Global Land Cover (FROM-GLC (Li et al., 2016), available at http://data.ess.tsinghua.edu.cn/data/Simulation/), which provides the most current (2010) and the finest-scale global future land use and land cover dynamics using four RCP scenarios (RCP2.6, RCP 4.5, RCP 6.0, and RCP 8.5) with eight general (cropland, forest, grassland, shrubland, water, impervious, bareland, and snow/ice) and 28 detailed land use types. For consistency with climatic data, we used the time period of 2010 and 2070 (average for 2061–2080, baseline is the year of 2010). We also selected three RCP scenarios (i.e. RCP 2.6, RCP 4.5, and RCP 8.5) as representative of the future land use scenarios. All land use data were resampled to a 30 arc-second (~1 km) resolution using a 'majority' interpolation in ArcGIS 10.2 (ESRI, 2011).

2.4. Species distribution model

Of the species distribution models, machine-learning algorithms (such as MaxEnt, Boosted Regression Trees, and Random Forests) frequently outperform regression based approaches (Beaumont et al., 2016). In this study, we used MaxEnt 3.3 (Phillips et al., 2006) because it has shown higher predictive accuracy compared with other methods across a wide range of sample sizes (Wisz et al., 2008), and performs well to estimate potential range shift of species (Hijmans and Graham, 2006). Using the recommended default parameters (i.e. regularization multiplier = 1, maximum number of backgrounds points = 10,000, maximum iterations = 500, and convergence threshold = 10^{-5}, Phillips et al., 2006 and http://www.cs.princeton.edu/~schapire/maxent/), we ran a 10-fold cross validation for the current and future (3GCMs × 3RCPs) potential distribution based on the assumption that current envelopes reflect species' environmental preferences, which will be retained under climate and land use change scenarios. We calculated the Boyce index (Boyce et al., 2002; Hirzel

et al., 2006) of the current potential predictions for evaluate predictive accuracy. Contrary to common evaluation measures, for example, AUC and TSS which may present problem for presence-only data, the Boyce index only requires presence data, and measures how much model predictions differ from a random distribution of the observed presences across the prediction gradients (Petitpierre et al., 2012). The Boyce index is fairly insensitive to species prevalence, it varies between −1 and 1. Positive values indicate a model which presents predictions that are consistent with the distribution of presences in the evaluation dataset, values closed to zero mean that the model is not different from a random model, and negative values indicate predicting poor quality areas where presences are more frequent (Hirzel et al., 2006).

We created binary distribution maps of suitable and unsuitable ranges from the continuous probability predictions of each species by using the threshold of 'maximum sensitivity and specificity (Max SSS)' (Liu et al., 2013). The Max SSS threshold can minimize the mean of the error rate and has been widely used in SDMs (Liu et al., 2013). We averaged the final binary result of each species for each RCP from 10 times prediction across 3 GCMs.

We evaluated the effect of climatic and land use variables on the Rhododendron distribution using the 'percent contribution' (relative contributions of the covariates to model results), a standard output of MaxEnt. We calculated the averaged contribution of climatic and land use variables for the narrow- and wide-ranging groups, respectively.
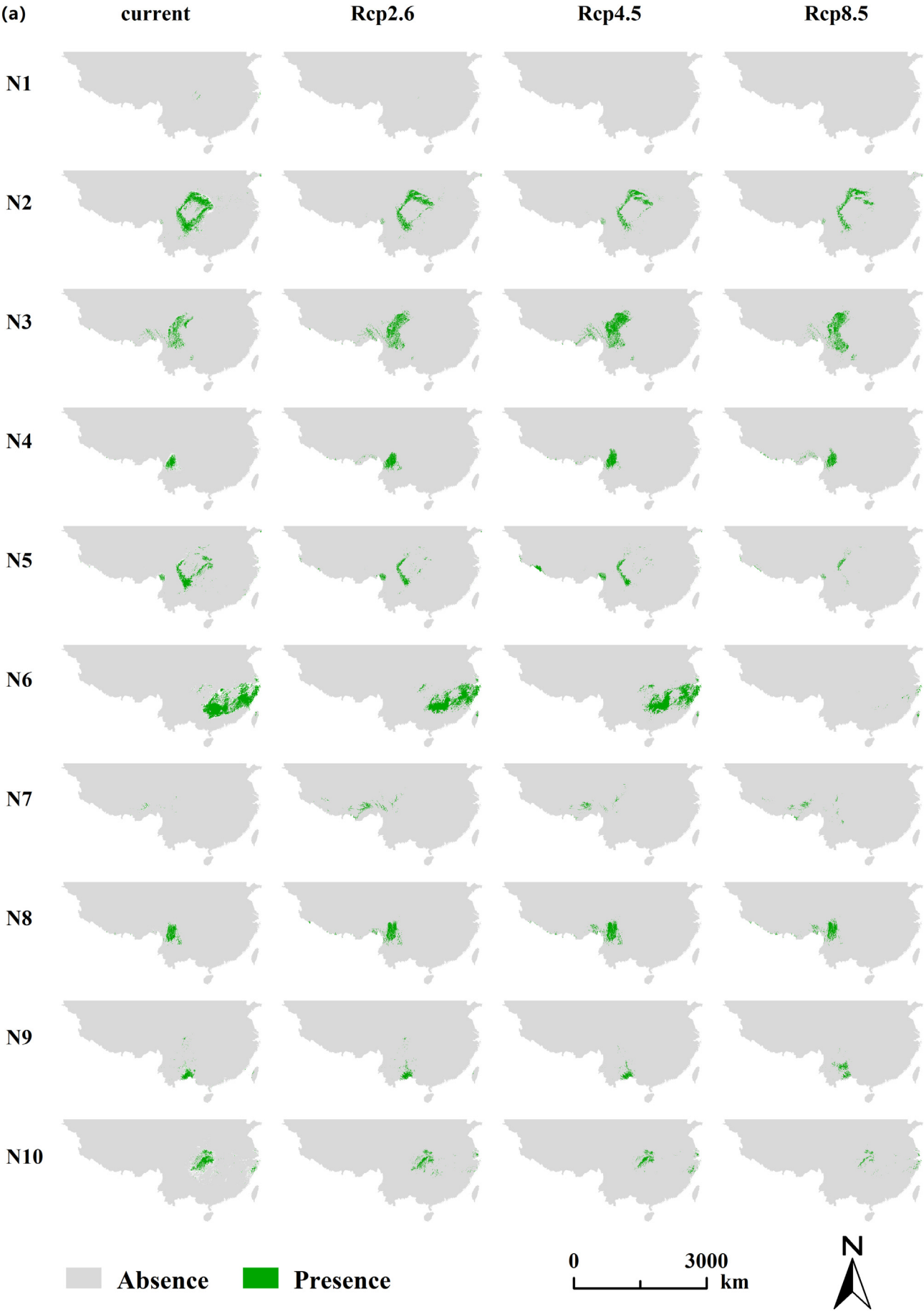
2.5. Geospatial analyses

To measure the predicted distribution change for each species, we projected the binary species distribution models (SDMs) onto Asia North Albers Equal-Area Conic projection in ArcGIS 10.2 (ESRI, 2011), and used three matrices to examine the magnitude and direction of shifts in potential distributions for each species, and divided them into narrow- and wide-ranging groups. Firstly, we calculated the change ratio following the eq. C = (A − B) / B, where C is the change ratio, while A and B are the future and current potential distribution area (km^2) of each species using a python-based GIS toolkit SDMtoolbox (Brown and Anderson, 2014). Secondly, we calculated distance and direction of core range shifts by comparing the centroids of current and future binary SDMs and the vectors between them using the SDMtoolbox (Brown and Anderson, 2014). Lastly, we calculated Schoener's D (Schoener, 1970; Broennimann et al., 2012) as the overlap between current and future distribution of Rhododendron species using 'ENMeval' package (Muscarella et al., 2014) in R 3.1 (R Core Team, 2015). The value of Schoener's D ranges from 0 (no overlap) to 1 (identical predictions). ENMeval calculated Schoener's D by comparing two normalized predicted probability distributions produced by MaxEnt with
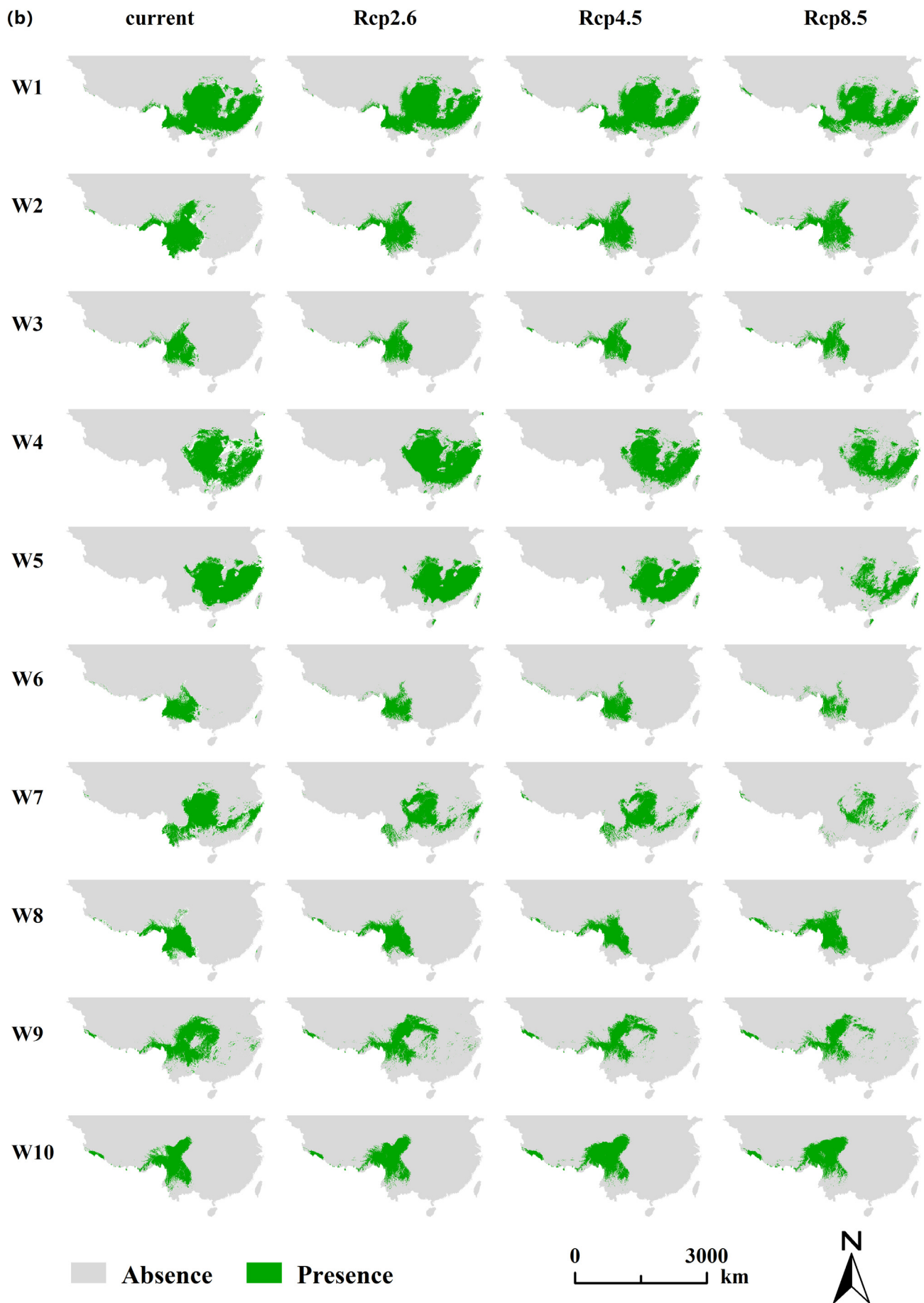
$$D(P_x, P_y) = 1 - \frac{1}{2} \sum_{n=i} |P_{x,i} - P_{y,i}|$$

where $P_{x,i}$ and $P_{y,i}$ represents the probability assigned by distribution model to grid cell i for current (x) and future (y) distribution of one species, respectively. We used the non-parametric Mann-Whitney U test to test if statistically significant differences were found in model performance and the three metrics.

Fig. 3. Distribution maps (binary results) of the narrow-ranging (a) and wide-ranging (b) groups under current and future (RCP 2.6, RCP 4.5, and RCP 8.5 in 2070) climate and land use conditions. Species codes are the same with Fig. 2.
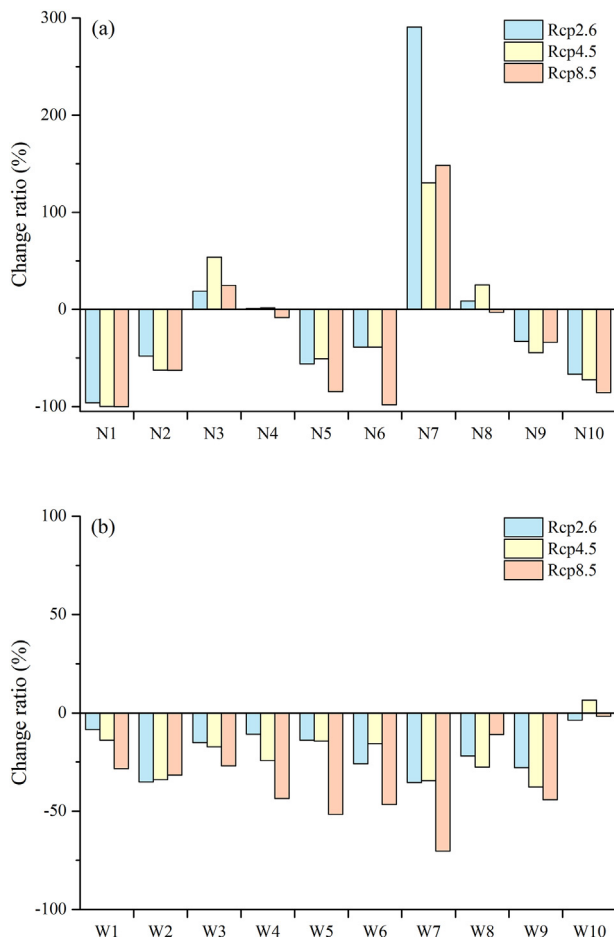
(a)

3. Results

3.1. Projected distributions of Rhododendrons

We obtained high-performing species distribution models for all 20 Rhododendron species with the Boyce index ranging from 0.73 to 0.99, and the presence probability and binary distribution maps of 20 species under current and future climate and land use changes in Figs. 2 and 3. Averaging across the six narrow-ranging species, which we predicted to experience range contractions, the distribution areas of the six species decreased with average ratios of −56.4%, −61.5%, and −77.5% from the current condition through to 2070 under the RCP 2.6, RCP 4.5, and RCP 8.5 projection scenarios (Fig. 4a). It worth noting that we predicted that one species (N1: *R. changii*) would go extinct, with a change ratio of −96.0%, −99.9%, and −100% under RCP 2.6, RCP 4.5 and RCP8.5 respectively (Fig. 4a-N1). Interestingly, we predicted the remaining four narrow-ranging species would experience range expansion in 2070 (Fig. 4a), with an average of change ratio at 79.7%, 52.6%, and 40.3% under RCP 2.6, RCP 4.5, and RCP 8.5. *R. viridescens* (N7) had the largest predicted distribution expansion with change ratios of 290.8%, 130.3%, and 148.3% under the three scenarios (Figs. 2a-N7, 3a-N7, and 4a-N7). Meanwhile, we predicted the distribution ranges of the wide-ranging group would decrease for all these species, with average change ratios of −19.8%, −21.3% and −35.6% under RCP 2.6, RCP 4.5 and RCP 8.5 (Fig. 4b). The distribution areas of *R. stamineum* (W7) would shrink −35.4%, −34.4%, and −70.3% in 2070, representing the largest drop in distribution
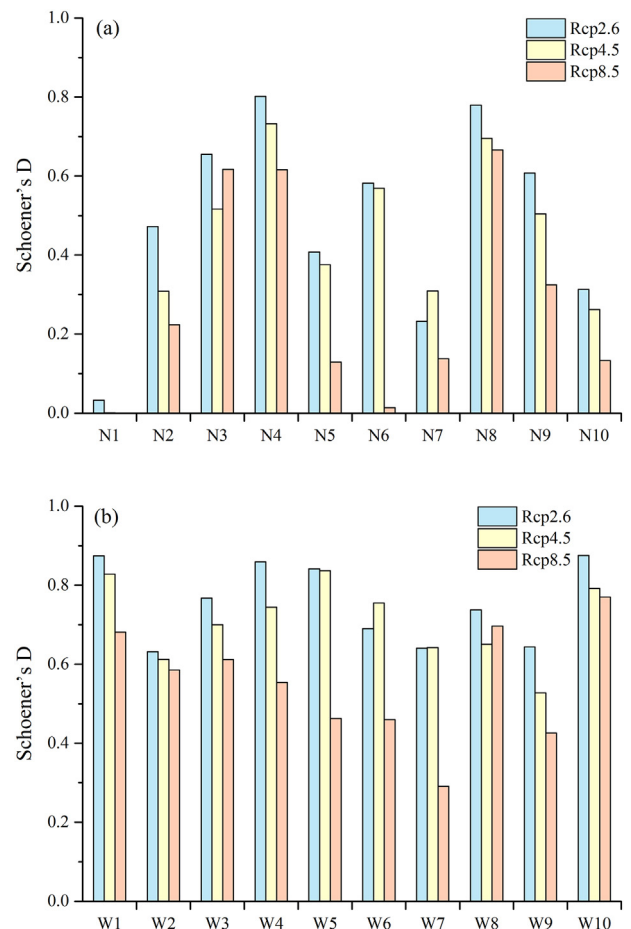
range among the wide-ranging species (Figs. 2b-W7, 3b-W7, and 4b-W7). The distribution range of *R. simsii* (W1) that had the largest geographical range size, would decline by −8.5%, −13.8%, and −28.4% (Figs. 2b-W1, 3b-W1, and 4b-W1).

The overlap between the current and future distributions for the narrow-ranging group (0.49, 0.42, and 0.29 under RCP 2.6, RCP 4.5, and RCP 8.5 respectively, Fig. 5a) were significantly ($p < 0.05$) lower than for the wide-ranging group, which was 0.76, 0.71, and 0.55 under RCP 2.6, RCP 4.5, and RCP 8.5 (Fig. 5b). The overlap between current and future species distribution decreased from the low to high RCP scenarios.
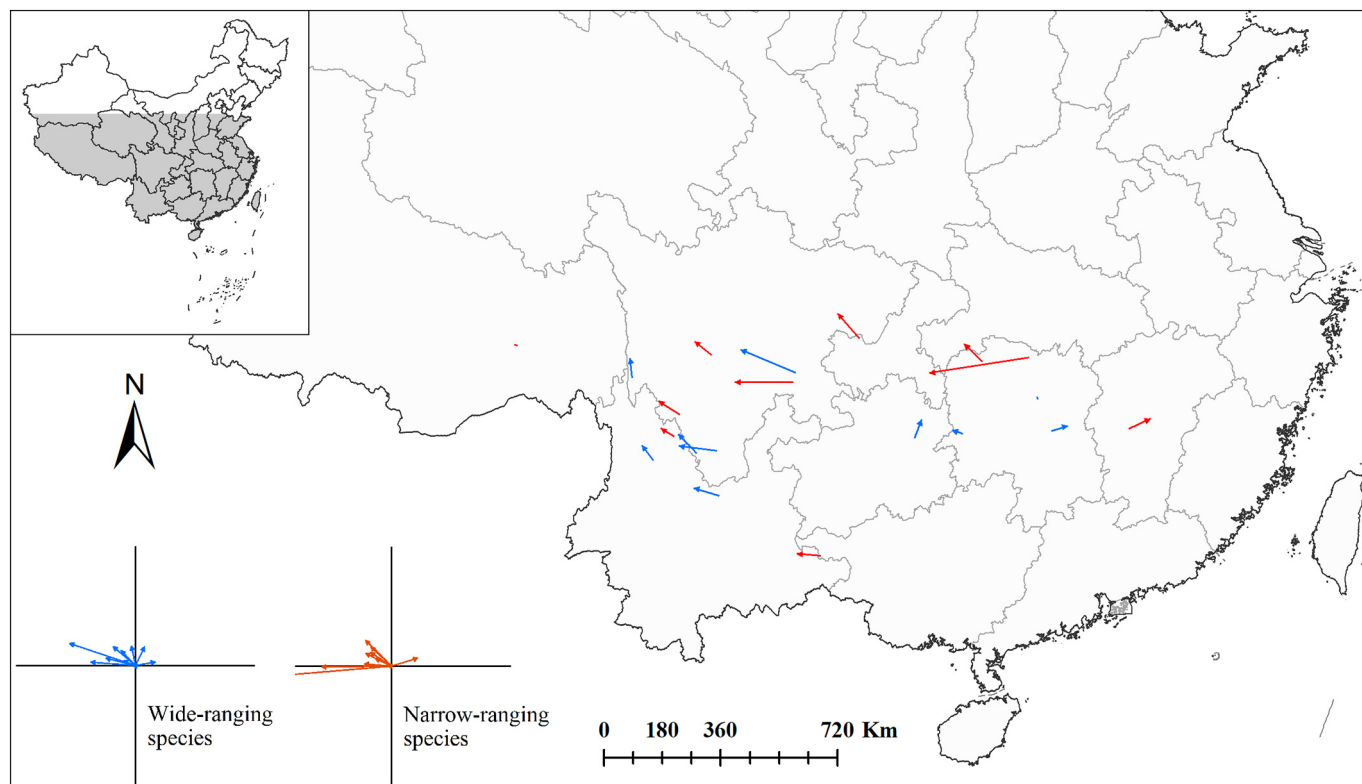
The core range shifts showed that 16 out of 20 species, regardless of their range sizes, would shift in a north-western direction (the shifting direction of species under RCP 2.6 – Fig. 6). We predicted the narrow-ranging species would shift 99.4 km, 219.5 km and 283.6 km, while the wide-ranging group would shift 73.4 km, 110.3 km, and 156.3 km under RCP 2.6, RCP 4.5 and RCP 8.5. There was no significant difference in distances between the two groups. The shift distance increased from the low to high RCP scenarios.

3.2. Relative contributions of climate and land use change to the future distribution of Rhododendrons

Both climatic and land use factors play a role in determining the distribution of Rhododendron species across the three scenarios (Fig. 7), with relative impacts that are species-specific. In general, climatic variables contributed greatly, with isothermality (Bio3) and precipitation of driest month (Bio14) providing 26.0% and 24.7% of the contribution to distribution of narrow-ranging species. Temperature seasonality

Fig. 4. Change ratios of distribution areas for the narrow-ranging (a) and wide-ranging (b) Rhododendron species under RCP 2.6, RCP 4.5, and RCP 8.5 in 2070. Species codes N1 to N10, and W1 to W10 are explained in Table 1.
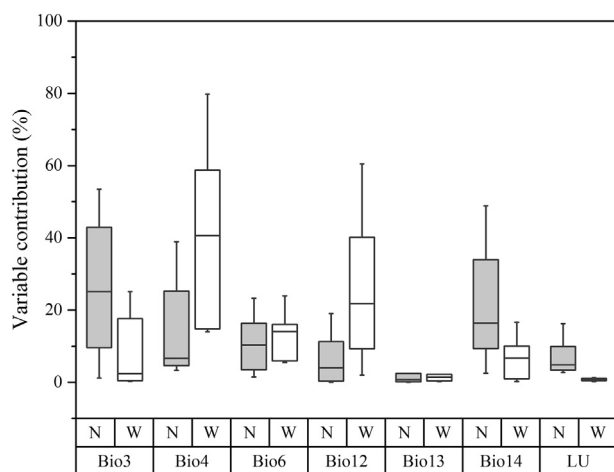

Fig. 5. Distribution overlap (measured by Schoener's D) between current and future distribution of (a) narrow-ranging and (b) wide-ranging Rhododendron species.

Fig. 6. Map of core range shifts depicts the predicted change on suitable areas (based on the centres of their distributions) of narrow-ranging (red arrow) and wide-ranging (blue arrow) Rhododendron species. Each line depicts the distance and direction of change at the centroid of distribution of species from current (2010, start of arrow) to 2070 (end of arrow) under RCP 2.6. The wind roses summarize the distance and direction of shift for two groups.

(Bio4) and annual precipitation (Bio12) were found relatively more important in projecting the wide-ranging species, with an average contribution of 41.1% and 25.3%, respectively. The minimum temperature of coldest month (Bio6) ranked the third important factor for both narrow-ranging and wide-ranging species, with the contribution being 14.7% and 12.8% respectively. In contrast, land use had a more significant contribution to models for narrow-ranging species, with an average of contribution of 8.3%, but varying between 2.9% to 27.1%. For wide-ranging species, the contribution of land use varied from 0.2% to 4.9%.

Fig. 7. Importance of climate and land use for the narrow-ranging (N) and wide-ranging (W) Rhododendron species.

4. Discussion

4.1. Future distribution of Rhododendrons under climate and land use change

Our results show that Rhododendron species generally will be negatively affected by the anticipated climatic and land use change for 2070, but some narrow-ranging species may be positively influenced. The variation of distribution change for narrow-ranging Rhododendron species is more significant than it is for the wide-ranging Rhododendron species. This results are consistent with previous studies which showed that some plant species may expand their distribution, while others experience range loss or even go extinct under global change (Pompe et al., 2008). In a broader sense, a species' geographical range can be used as a proxy for its ecological well-being. Species with small ranges are regarded as more vulnerable to extinction (Davies et al., 2009), because species with a limited distribution typically possess narrower ecological tolerances, and even slight environmental change may affect those species (Murray et al., 2011). Species with wider distribution ranges are expected to be more resilient to climate and land use change (Williams et al., 2006; Carrillo-Angeles et al., 2016). However, impacts of climate and land use change may have a disproportionate effect on some closely related species or clades (Zhang et al., 2017). It is possible that narrow-ranging species, which occupy warm climatological niches, will persist or even benefit from the climate change (Barry et al., 1995; Frishkoff et al., 2016), while other narrow ranging species may go extinct. In this study, we grouped narrow- and wide-ranging species based on their geographical ranges. In a previous study we found that species with narrow geographical ranges may have large elevational ranges (Yu et al., 2017a). The results of the current study confirmed that species which are both geographically and elevationally narrow ranging (e.g. *R. changii* (N1) in this study) will be most vulnerable

under climate and land use change. Species that have a narrow geographical range, but a relatively wide elevational range (e.g. *R. viridescens* (N7) in this study), may have a wider tolerance to climate variability, which implies a possibility of future expansion (Valladares et al., 2014), We suggest that the elevational range and geographical range should be considered together when evaluating the distribution change of narrow-ranging species. Lenoir and Svenning (2015) also advocated using multi-facetted approaches, at least two geographical dimensions (latitude and elevation) simultaneously, to assess distribution shifts or abundance change either at the leading edge, the trailing edge or the optimum positions.

Furthermore, individual species varies greatly in their rates of change under future climate and land use change, which will be determined by multiple internal species traits (e.g. dispersal capacity), their tolerances to environmental stresses (Ye et al., 2018), and the external drivers of change (Chen et al., 2011). And the combined environmental change would exhibit strong spatial heterogeneity in the future. For instance, *R. viridescens* (N7) is distributed in the southeast Tibet, where human disturbance is very low and consequently land use change over there is also not significant. Huang et al. (2016) showed that an increase in precipitation tended to enhance vegetation growth during warming periods on the Qinghai-Tibet Plateau from 1986 to 2011. Our results showed that the increase trend in both temperature and precipitation would continue into the future on the Qinghai-Tibet Plateau (Fig. A.1). Therefore, we speculate that *R. viridescens* (N7) is one of the species who would benefit from the future climate change. In the meantime, future distribution of the same species also varies between scenarios, besides the tolerance to environmental stress we mentioned above, the difference stems from the formation of three RCPs. In our case, RCP 2.6 might be the most suitable scenarios for *R. viridescens* (N7) growing, which would cause a larger expansion. The temperature and precipitation change under RCP 4.5 and RCP 8.5 might be too intense to restrain growth of *R. viridescens* (N7) relative to RCP 2.6.

With the increase of greenhouse gas emissions, it is supposed to have higher rates of warming globally, including China (https://www.ipcc.ch/index.htm). We observed a prominent trend of increasing temperature (Fig. A.1-Bio 6), and various precipitation changes for 2070 in China (Fig. A.1-Bio12 and Bio13). The variability of temperature (Fig. A.1-Bio3 and Bio4) and precipitation (Fig. A.1-Bio13 and Bio14) would increase from RCP 2.6 to RCP 8.5. Rhododendrons, as a typical alpine and subalpine group, are highly sensitive to the temperature variation, and vulnerable to the increasing temperature (Yu et al., 2017a), they thus shift further and more rapidly under higher emission scenario (RCP 8.5) relative to lower emission (RCP2.6).

In addition, poleward shifts and shifts to higher elevations are the most frequent types of range shifts that have been reported in response to contemporary climate change (Chen et al., 2011). Meanwhile, the number of reports documenting other types of range shifts, such as in east-west directions across longitudes or, even more unexpectedly, towards tropical latitudes and lower elevations is rapidly increasing (Lenoir and Svenning, 2015). We speculate that the north-westward shift observed in our study can be mainly attributed to the following aspects: on one hand, climate warming has caused the northern shifts in optimal conditions for most species (Boisvert-Marsh et al., 2014). Based on the comparison of current and future climate change in our study area (Fig. A.1), Rhododendrons are also expected to shift northward with the warming trend, which have been reported in alpine plants (Grabherr et al., 1994). On the other hand, the high mountains are mainly located in the west of China (Fig. 1), while Rhododendrons are mainly distributed along mountain ranges (Yu et al., 2017b), and plant species inhabiting mountain slopes tend to move uphill (Sugden, 2018). We thus infer that the distribution of mountains, internal traits of Rhododendrons, coupling with the external environmental changes of China would jointly cause the north-westward migration of Rhododendrons.

4.2. Role of climate and land use change in regulating the distribution of Rhododendrons

Our results indicate that climate change has a more significant effect than land use change on the distribution of Rhododendron species. There are three possible reasons, the first one is a scale issue. Previous studies proposed that land use change may outweigh the effect of climate change on species and ecosystem at finer scales (habitat to landscape, <20 years), while climate change has been proven to be more important at broader spatial and temporal scale (regional to continental, >50 years) (Sirami et al., 2017). In our case, the influence of climate change may override the effect of land use change, and play a more prominent role in distribution of Rhododendrons at the continental extent and the 60-year prediction horizon. A second reason could be that Rhododendrons generally grow at middle to high elevation regions, where climatic change is more dominant. Meanwhile, the relatively more intense effects of land use on narrow-ranging Rhododendron species confirm that narrow-ranging species tended to be affected by land use (Walker and Preston, 2006; Newbold et al., 2013), especially those that grow at low altitudes. The pronounced effect of land use change on plant distribution at the low altitude has been demonstrated in other studies (Feeley and Silman, 2010). Thirdly, it could be that there are strong correlations between land use change and climate change. It is difficult to test for collinearity issues between categorical and continuous variables, and hence that test was not performed here, but it seems reasonable to assume that climate change will affect how land use changes.

4.3. Implications for Rhododendrons conservation in China

Rhododendrons play a vital role in providing the structure of plant communities which support a wealth of biodiversity in the Himalayas. The generally shrinking distribution of most Rhododendron species would lead to potentially negative consequences for biodiversity and ecosystem functioning in the Himalayas. To the best of our knowledge, there is currently only one study about the future distribution of Rhododendrons, in which Kumar (2012) concluded that the distribution of Rhododendron species will shrink considerably under envisaged climate change scenarios in the Sikkim region of the Himalayas. However, this conclusion was based on the prediction of tree species of Rhododendrons with a total of 63 occurrences, and land use change was not included. Ma et al. (2014) reported that the rising demand for farming land, construction of roadways, hydro-electric power stations, and more recently developments associated with the tourism industry, have all collectively placed considerable pressure on Rhododendron species in China. The projected extinction for *R. changii* (N1) in our study can be regarded as a representative narrow-ranging species – where land use has a great influence on its distribution (variable importance was 9.9%). This is consistent with the description of The Red List of Rhododendrons - '*R. changii* (N1) is restricted to a single locality (Jinfoshan, Chongqing) which is a popular tourist site, and the forest habitat is under significant pressure and disturbance' (Gibbs et al., 2011). We also noticed that *R. changii* (N1) has a very narrow elevational range which is from 2000 to 3000 m, which implies that species on mountain ranges with narrow geographical and elevational ranges will experience higher risks of extinction in the future. In addition, we emphasize that *R. changii* (N1) is only one of the many Rhododendron species which have a small population, and most of these rare species did not even qualify as candidate model species because of the limited number of available records. Those species are actually more likely to be affected by either climate or land use change. Of the 246 endemic species, there are 27 species whose occurrence records contained <10 entries. Most of these species are critically endangered. Ma et al. (2014) conducted a field investigation for the conservation status on 10 critically endangered or endangered Rhododendron species in China. They concluded that species that grow at low altitudes and in disturbed habitats, should be given priority for ex- and in-situ

conservation. We emphasize that indeed there is an urgent need for more comprehensive field surveys of Rhododendron species. Besides the critically endangered species ranked by The Red List of Rhododendrons (Gibbs et al., 2011), attention also should be given to endemic species that have narrow elevational ranges.

4.4. Uncertainty in predictions of Rhododendron distribution

Our study established a good example for predicting the distribution of plant species under both future climate and land use change scenarios. However, our results may also be affected by several sources of uncertainties. Firstly, the accuracy of the input climate and land use data as well as the species occurrence data can be one of the main sources of uncertainties (Rocchini et al., 2011). Secondly, the predictions may also be affected by model uncertainty (Elith and Leathwick, 2009). For example, using an ensemble model may improve the modelling performance than using MaxEnt alone. Thirdly, we assumed that all species can move freely to climatically suitable areas, by which the real effects of climate and land use change were simplified (Engler et al., 2009; Ye et al., 2018). In reality, a species may have failed to disperse due to geographic barriers, or be excluded from an area due to competition, although the method we used was optimized for predicting realized distributions (Phillips and Dudik, 2008). Therefore, further research is required to complement our findings, such as how to integrate dispersal capability and landscape fragmentation into the modelling. Nevertheless, our results do provide important information about the potential distribution of narrow-ranging and wide-ranging Rhododendrons under the future climate and land use changes.
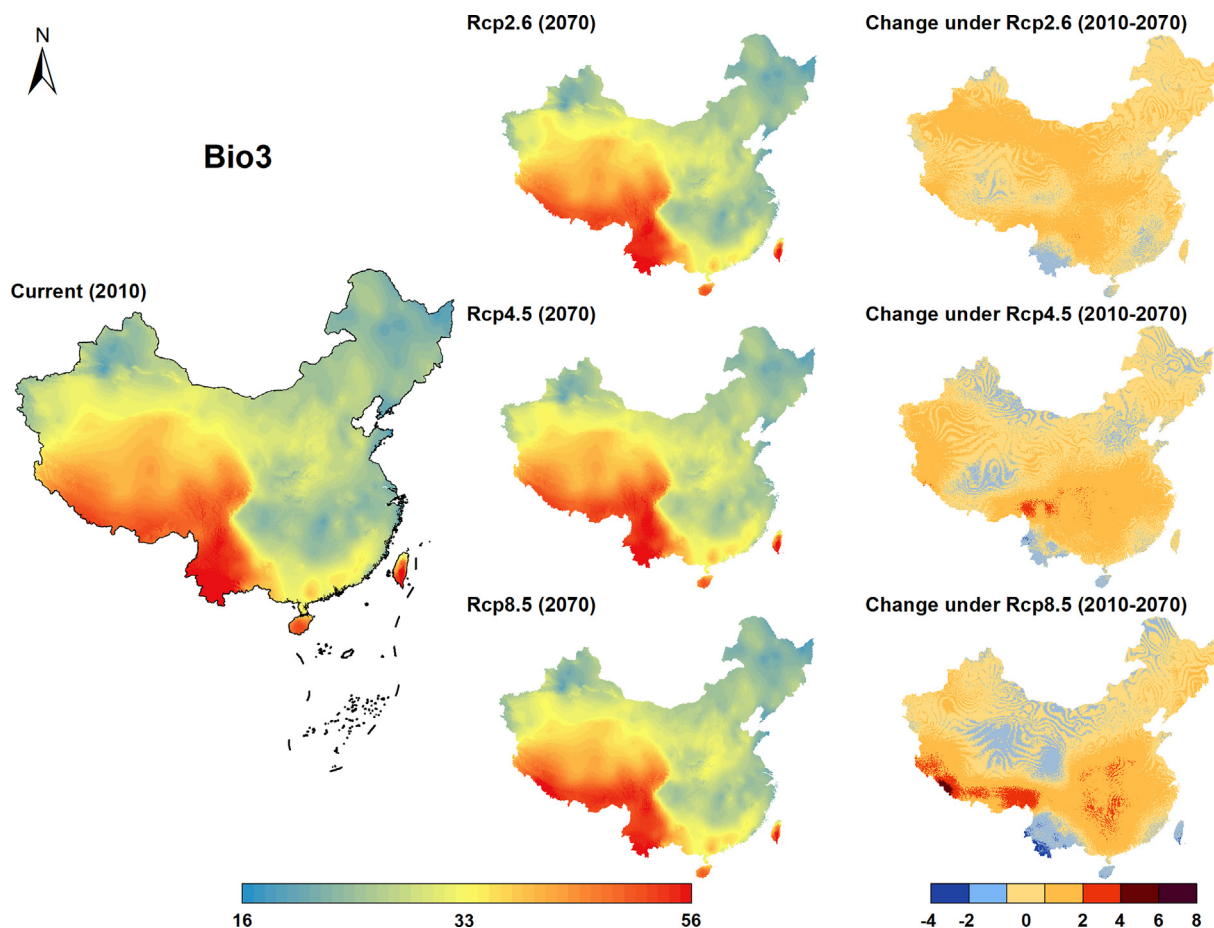
5. Conclusions

This study predicted the potential impacts of future climate and land use change on the distribution of narrow- and wide-ranging Rhododendron species, and estimated their relative contribution in China. The results showed that the distribution areas of six narrow-ranging species would decrease, of which one species would go extinct. The remaining four narrow-ranging species would experience range expansion. Distribution of all the wide-ranging Rhododendron species would decrease. All Rhododendrons will shift to the northwest. We conclude that Rhododendron species generally will be negatively affected by the climatic and land use change expected in 2070 from the three scenarios evaluated in this study, but some narrow-ranging species may be positively influenced. Narrow-ranging Rhododendron species are more vulnerable compared to wide-ranging Rhododendron species. This study demonstrated that the effects of climate and land use change on alpine and subalpine plant species is species-specific, thereby strengthening our understanding of the impacts of climate and land use change on plant distribution.

Appendix A

Fig. A.1. Spatial pattern of the current, future climatic variables (predicted by BCC-CSM1-1), and change between 2010 and 2070.

References

Barry, J.P., Baxter, C.H., Sagarin, R.D., Gilman, S.E., 1995. Climate-related, long-term faunal changes in a California rocky intertidal community. Science 267, 672–675.

Beaumont, L.J., Graham, E., Duursma, D.E., Wilson, P.D., Cabrelli, A., Baumgartner, J.B., Hallgren, W., Esperón-Rodríguez, M., Nipperess, D.A., Warren, D.L., Laffan, S.W., VanDerWal, J., 2016. Which species distribution models are more (or less) likely to project broad-scale, climate-induced shifts in species ranges? Ecol. Model. 342, 135–146.

Boisvert-Marsh, L., Périé, C., de Blois, S., 2014. Shifting with climate? Evidence for recent changes in tree species distribution at high latitudes. Ecosphere 5, 1–33.

Boyce, M.S., Vernier, P.R., Nielsen, S.E., Schmiegelow, F.K.A., 2002. Evaluating resource selection functions. Ecol. Model. 157, 281–300.

Broennimann, O., Fitzpatrick, M.C., Pearman, P.B., Petitpierre, B., Pellissier, L., Yoccoz, N.G., Thuiller, W., Fortin, M.-J., Randin, C., Zimmermann, N.E., Graham, C.H., Guisan, A., 2012. Measuring ecological niche overlap from occurrence and spatial environmental data. Glob. Ecol. Biogeogr. 21, 481–497.

Brook, B.W., Sodhi, N.S., Bradshaw, C.J.A., 2008. Synergies among extinction drivers under global change. Trends Ecol. Evol. 23, 453–460.

Brown, J.L., Anderson, B., 2014. SDMtoolbox: a python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. Methods Ecol. Evol. 5, 694–700.

Carrillo-Angeles, I.G., Suzán-Azpiri, H., Mandujano, M.C., Golubov, J., Martínez-Ávalos, J.G., 2016. Niche breadth and the implications of climate change in the conservation of the genus *Astrophytum* (Cactaceae). J. Arid Environ. 124, 310–317.

Chen, I.C., Hill, J.K., Ohlemuller, R., Roy, D.B., Thomas, C.D., 2011. Rapid range shifts of species associated with high levels of climate warming. Science 333, 1024–1026.

Cleary, D.F.R., Mooers, A.O., 2006. Burning and logging differentially affect endemic vs. widely distributed butterfly species in Borneo. Divers. Distrib. 12, 409–416.

Davies, T.J., Purvis, A., Gittleman, J.L., 2009. Quaternary climate change and the geographic ranges of mammals. Am. Nat. 174, 297–307.

Elith, J., Leathwick, J.R., 2009. Species distribution models: ecological explanation and prediction across space and time. Annu. Rev. Ecol. Evol. Syst. 40, 677–697.

Engler, R., Randin, C.F., Vittoz, P., Czáka, T., Beniston, M., Zimmermann, N.E., Guisan, A., 2009. Predicting future distributions of mountain plants under climate change: does dispersal capacity matter? Ecography 32, 34–45.

ESRI, 2011. ArcGIS Desktop: Release 10. Environmental Systems Research Institute, Redlands, CA.

Feeley, K.J., Silman, M.R., 2010. Land-use and climate change effects on population size and extinction risk of Andean plants. Glob. Chang. Biol. 16, 3215–3222.

Foley, J.A., Defries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N., Snyder, P.K., 2005. Global consequences of land use. Science 309, 570–574.

Frishkoff, L.O., Karp, D.S., Flanders, J.R., Zook, J., Hadly, E.A., Daily, G.C., M'Gonigle, L.K., 2016. Climate change and habitat conversion favour the same species. Ecol. Lett. 19, 1081–1090.

Gallagher, R.V., 2016. Correlates of range size variation in the Australian seed-plant flora. J. Biogeogr. 43, 1287–1298.

Gibbs, D., Chamberlain, D., Argent, G., 2011. The Red List of Rhododendrons. Botanic Gardens Conservation International, Richmond, UK.

Grabherr, G., Gottfried, M., Pauli, H., 1994. Climate effects on mountain plants. Nature 369, 448.

Harcourt, A.H., Coppeto, S.A., Parks, S.A., 2002. Rarity, specialization and extinction in primates. J. Biogeogr. 29, 445–456.

Hickling, R., Roy, D.B., Hill, J.K., Fox, R., Thomas, C.D., 2006. The distributions of a wide range of taxonomic groups are expanding polewards. Glob. Chang. Biol. 12, 450–455.

Hijmans, R.J., Graham, C.H., 2006. The ability of climate envelope models to predict the effect of climate change on species distributions. Glob. Chang. Biol. 12, 2272–2281.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25, 1965–1978.

Hirzel, A.H., Le Lay, G., Helfer, V., Randin, C., Guisan, A., 2006. Evaluating the ability of habitat suitability models to predict species presences. Ecol. Model. 199, 142–152.

Huang, K., Zhang, Y., Zhu, J., Liu, Y., Zu, J., Zhang, J., 2016. The influences of climate change and human activities on vegetation dynamics in the Qinghai-Tibet Plateau. Remote Sens. 8, 876.

Köster, N., Kreft, H., Nieder, J., Barthlott, W., 2013. Range size and climatic niche correlate with the vulnerability of epiphytes to human land use in the tropics. J. Biogeogr. 40, 963–976.

Kumar, P., 2012. Assessment of impact of climate change on *Rhododendrons* in Sikkim Himalayas using Maxent modelling: limitations and challenges. Biodivers. Conserv. 21, 1251–1266.

Lenoir, J., Svenning, J.C., 2015. Climate-related range shifts - a global multidimensional synthesis and new research directions. Ecography 38, 15–28.

Lenoir, J., Gegout, J.C., Marquet, P.A., de Ruffray, P., Brisse, H., 2008. A significant upward shift in plant species optimum elevation during the 20th century. Science 320, 1768–1771.

Li, X., Yu, L., Sohl, T., Clinton, N., Li, W., Zhu, Z., Liu, X., Gong, P., 2016. A cellular automata downscaling based 1 km global land use datasets (2010−2100). Sci. Bull. 61, 1651–1661.

Liu, C., White, M., Newell, G., Pearson, R., 2013. Selecting thresholds for the prediction of species occurrence with presence-only data. J. Biogeogr. 40, 778–789.

Ma, Y., Nielsen, J., Chamberlain, D.F., Li, X., Sun, W., 2014. The conservation of *Rhododendrons* is of greater urgency than has been previously acknowledged in China. Biodivers. Conserv. 23, 3149–3154.

Murray, K.A., Rosauer, D., McCallum, H., Skerratt, L.F., 2011. Integrating species traits with extrinsic threats: closing the gap between predicting and preventing species declines. Proc. R. Soc. B Biol. Sci. 278, 1515–1523.

Muscarella, R., Galante, P.J., Soley-Guardia, M., Boria, R.A., Kass, J.M., Uriarte, M., Anderson, R.P., 2014. ENMeval: an R package for conducting spatially independent evaluations and estimating optimal model complexity for MAXENT ecological niche models. Methods Ecol. Evol. 5, 1198–1205.

Newbold, T., Scharlemann, J.P., Butchart, S.H., Sekercioglu, C.H., Alkemade, R., Booth, H., Purves, D.W., 2013. Ecological traits affect the response of tropical forest bird species to land-use intensity. Proc. R. Soc. B Biol. Sci. 280, 8.

Oliver, T.H., Morecroft, M.D., 2014. Interactions between climate change and land use change on biodiversity: attribution problems, risks, and opportunities. Wiley Interdiscip. Rev. Clim. Chang. 5, 317–335.

Parmesan, C., 2006. Ecological and evolutionary responses to recent climate change. Annu. Rev. Ecol. Evol. Syst. 37, 637–669.

Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421, 37–42.

Pearson, R.G., Stanton, J.C., Shoemaker, K.T., Aiello-Lammens, M.E., Ersts, P.J., Horning, N., Fordham, D.A., Raxworthy, C.J., Ryu, H.Y., McNees, J., Akçakaya, H.R., 2014. Life history and spatial traits predict extinction risk due to climate change. Nat. Clim. Chang. 4, 217–221.

Petitpierre, B., Kueffer, C., Broennimann, O., Randin, C., Daehler, C., Guisan, A., 2012. Climatic niche shifts are rare among terrestrial plant invaders. Science 335, 1344–1348.

Phillips, S.J., Dudik, M., 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography 31, 161–175.

Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecol. Model. 190, 231–259.

Pompe, S., Hanspach, J., Badeck, F., Klotz, S., Thuiller, W., Kuhn, I., 2008. Climate and land use change impacts on plant distributions in Germany. Biol. Lett. 4, 564–567.

Purvis, A., Gittleman, J.L., Cowlishaw, G., Mace, G.M., 2000. Predicting extinction risk in declining species. Proc. R. Soc. B Biol. Sci. 267, 1947–1952.

R Core Team, 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austriahttp://www.R-project.org.

Rocchini, D., Hortal, J., Lengyel, S., Lobo, J.M., Jimenez-Valverde, A., Ricotta, C., Bacaro, G., Chiarucci, A., 2011. Accounting for uncertainty when mapping species distributions: the need for maps of ignorance. Prog. Phys. Geogr. 35, 211–226.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., Wall, D.H., 2000. Biodiversity - global biodiversity scenarios for the year 2100. Science 287, 1770–1774.

Schoener, T.W., 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. Ecology 51, 408–418.

Sheth, S.N., Angert, A.L., 2014. The evolution of environmental tolerance and range size: a comparison of geographically restricted and widespread Mimulus. Evolution 68, 2917–2931.

Sirami, C., Caplat, P., Popy, S., Clamens, A., Arlettaz, R., Jiguet, F., Brotons, L., Martin, J.-L., 2017. Impacts of global change on species distributions: obstacles and solutions to integrate climate and land use. Glob. Ecol. Biogeogr. 26, 385–394.

Slatyer, R.A., Hirst, M., Sexton, J.P., 2013. Niche breadth predicts geographical range size: a general ecological pattern. Ecol. Lett. 16, 1104–1114.

Sugden, A.M., 2018. Different responses to climate change in mountain plants. Science 359, 881.

Taylor, K.E., Stouffer, R.J., Meehl, G.A., 2012. An overview of CMIP5 and the experiment design. Bull. Am. Meteorol. Soc. 93, 485–498.

Thuiller, W., Lavorel, S., Araujo, M.B., 2005. Niche properties and geographical extent as predictors of species sensitivity to climate change. Glob. Ecol. Biogeogr. 14, 347–357.

Titeux, N., Henle, K., Mihoub, J.B., Regos, A., Geijzendorffer, I.R., Cramer, W., Verburg, P.H., Brotons, L., 2016. Biodiversity scenarios neglect future land-use changes. Glob. Chang. Biol. 22, 2505–2515.

Travis, J.M.J., 2003. Climate change and habitat destruction: a deadly anthropogenic cocktail. Proc. R. Soc. B Biol. Sci. 270, 467–473.

Valladares, F., Matesanz, S., Guilhaumon, F., Araujo, M.B., Balaguer, L., Benito-Garzon, M., Cornwell, W., Gianoli, E., van Kleunen, M., Naya, D.E., Nicotra, A.B., Poorter, H., Zavala, M.A., 2014. The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. Ecol. Lett. 17, 1351–1364.

van Vuuren, D.P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K., Hurtt, G.C., Kram, T., Krey, V., Lamarque, J.-F., Masui, T., Meinshausen, M., Nakicenovic, N., Smith, S.J., Rose, S.K., 2011. The representative concentration pathways: an overview. Clim. Chang. 109, 5–31.

Walker, K.J., Preston, C.D., 2006. Ecological predictors of extinction risk in the Flora of Lowland England, UK. Biodivers. Conserv. 15, 1913–1942.

Weyant, J., Azar, C., Kainuma, M., Jiang, K.J., Nakicenovic, N., Shukla, P.R., Rovere, E.L., G, Y., 2009. Report of 2.6 Versus 2.9 Watts/m2 RCPP Evaluation Panel.

Williams, Y.M., Williams, S.E., Alford, R.A., Waycott, M., Johnson, C.N., 2006. Niche breadth and geographical range: ecological compensation for geographical rarity in rainforest frogs. Biol. Lett. 2, 532–535.

Wisz, M.S., Hijmans, R.J., Li, J., Peterson, A.T., Graham, C.H., Guisan, A., Distribut, N.P.S., 2008. Effects of sample size on the performance of species distribution models. Divers. Distrib. 14, 763–773.

Xu, J.C., Grumbine, R.E., Shrestha, A., Eriksson, M., Yang, X.F., Wang, Y., Wilkes, A., 2009. The melting Himalayas: cascading effects of climate change on water, biodiversity, and livelihoods. Conserv. Biol. 23, 520–530.

Ye, X., Yu, X., Yu, C., Tayibazhaer, A., Xu, F., Skidmore, A.K., Wang, T., 2018. Impacts of future climate and land cover changes on threatened mammals in the semi-arid Chinese Altai Mountains. Sci. Total Environ. 612, 775–787.

Yu, F.Y., Wang, T.J., Groen, T.A., Skidmore, A.K., Yang, X.F., Geng, Y.Y., Ma, K.P., 2015. Multi-scale comparison of topographic complexity indices in relation to plant species richness. Ecol. Complex. 22, 93–101.

Yu, F.Y., Groen, T.A., Wang, T.J., Skidmore, A.K., Huang, J.H., Ma, K.P., 2017a. Climatic niche breadth can explain variation in geographical range size of alpine and subalpine plants. Int. J. Geogr. Inf. Sci. 31, 190–212.

Yu, F.Y., Skidmore, A.K., Wang, T.J., Huang, J.H., Ma, K.P., Groen, T.A., 2017b. Rhododendron diversity patterns and priority conservation areas in China. Divers. Distrib. 23, 1143–1156.

Zhang, J., Nielsen, S.E., Chen, Y., Georges, D., Qin, Y., Wang, S.-S., Svenning, J.-C., Thuiller, W., 2017. Extinction risk of North American seed plants elevated by climate and land-use change. J. Appl. Ecol. 54, 303–312.